ZooKeys 100: 149–169 (2011)
doi: 10.3897/zookeys.100.1524
www.zookeys.org

RESEARCH ARTICLE

A peer-reviewed open-access journal
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Sub-fossil beetle assemblages associated with the "mammoth fauna" in the Late Pleistocene localities of the Ural Mountains and West Siberia

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Academic editor: *Hans Turin* | Received 30 November 2009 | Accepted 31 May 2010 | Published 20 May 2011

Citation: Zinovyev E (2011) Sub-fossil beetle assemblages associated with the "mammoth fauna" in the Late Pleistocene localities of the Ural Mountains and West Siberia. In: Kotze DJ, Assmann T, Noordijk J, Turin H, Vermeulen R (Eds) Carabid Beetles as Bioindicators: Biogeographical, Ecological and Environmental Studies. ZooKeys 100: 149–169. doi: 10.3897/zookeys.100.1524

Abstract

The distribution of beetles at the end of the Middle Pleninglacial (=terminal Quaternary) was examined based on sub-fossil material from the Ural Mountains and Western Siberia, Russia. All relevant localities of fossil insects have similar radiocarbon dates, ranging between 33,000 and 22,000 C^{14} years ago. Being situated across the vast territory from the southern Ural Mountains in the South to the middle Yamal Peninsula in the North, they allow latitudinal changes in beetle assemblages of that time to be traced. These beetles lived simultaneously with mammals of the so-called "mammoth fauna" with mammoth, bison, and wooly rhinoceros, the often co-occurring mega-mammalian bones at some of the sites being evidence of this. The beetle assemblages found between 59° and 57°N appear to be the most interesting. Their bulk is referred to as a "mixed" type, one which includes a characteristic combination of arcto-boreal, boreal, steppe and polyzonal species showing no analogues among recent insect complexes. These peculiar faunas seem to have represented a particular zonal type, which disappeared since the end of the Last Glaciation to arrive here with the extinction of the mammoth biota. In contrast, on the sites lying north of 60°N, the beetle communities were similar to modern sub-arctic and arctic faunas, yet with the participation of some sub-boreal steppe components, such as *Poecilus ravus* Lutshnik and *Carabus sibiricus* Fischer-Waldheim. This information, when compared with our knowledge of synchronous insect faunas from other regions of northern Eurasia, suggests that the former distribution of beetles in this region could be accounted for both by palaeo-environmental conditions and the impact of grazing by large ruminant mammals across the so-called "mammoth savannas".

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Keywords
Carabidae, Coleoptera, sub-fossil beetles, fauna change, insect assemblages

Introduction

One of the main tasks of any zoological investigation is the study of the influence of environmental factors on the structure of communities, including changes in insect faunas. These changes may be estimated from modern faunas. But it is necessary to study such factors, which could define the specific structure of insect communities in the past.

With respect to research on palaeo-entomological processes, it is extremely difficult to estimate the character of external influences on the structure of communities, because there are no real opportunities to inspect them directly. It is only possible to make reconstructions, which are based on the analysis of sub-fossil insect assemblages found in Quaternary strata. The term "sub-fossil" means, that insect remains are presented in these layers by isolated chitin fragments not yet fossilized. Present ecological requirements of these species can be extrapolated to the period of the past investigated; the conclusions of which can be compared with results of palaeo-botanical analysis and studies of mega and small mammals. The comparison of these conclusions allows a reconstruction to be made of palaeoenvironmental conditions prevailing in the given territory in the analyzed period of the past.

The aim of this study is to try to explain peculiarities of the insect faunas in relation with the paleoenvironmental conditions of the terminal phase of the Late Pleistocene and estimate the factors possibly determining the composition of insect species in the past, including the influence of the large herbivorous mammals.

Materials

To this end, I took some synchronous sites situated in the vast territory from the Jamal peninsula in the North up to vicinities of Ekaterinburg city in the South. Radiocarbon dating confirmed the synchrony of these sites. The period of investigations covers the end of the Late Pleistocene including terminal phase of Middle Pleninglacial period and the beginning of the Late Pleninglacial or Late Glacial Maximum (LGM). Chronologically this time corresponds to the end of Maritime Isotope Stage (MIS) 3 and the beginning of MIS 2; 33,000–22,000 years Before Present (BP). This period is considered by geologists as the most severe time of the Late Pleistocene and characterized by a cooler-than-present climate which fluctuated heavily on time scales of a few thousand years (Adams et al. 1999; Adams and Faure 1999; Arkhipov and Volkova 1994; Astakhov 2009; Bos et al. 2004).

The work is based on sub-fossil material obtained from 13 sites scattered over the large territory of the Ural Mountains and West Siberia (Figure 1; Table 1). Sub-fossil

insect remains were found in deposits exposed both in quarries and in river banks. Field sampling was done using the standard techniques in Kiselev (1987). Geologists provided geological descriptions of the sites and their provisional dating; most samples were radiocarbon-dated (Table 1). Laboratory treatment and the subsequent identification of fossil specimens were performed at the Institute of Plant and Animal Ecology in Ekaterinburg. The classification of the sub-fossil insect faunas used is that proposed by the author (Zinovyev 2006).

Results

All studied insect faunas occurred in the interval between 33,000 and 22,000 C^{14} yr. BP (Table 1), the terminal phase of the Middle Pleninglacial (MIS 3). These studies cover the vast territory between 67° and 57°N. I tried to trace elements of latitudinal zonality and estimate factors affecting natural ecosystems and insect faunas.

According to the classification by Zinovyev (2006), the studied faunas can be referred to as arctic, sub-arctic, "mixed" and boreal types.

Only faunas of the arctic type were found at the sites lying north of 61°N latitude (sites 1–3 in Table 1). The main characteristics of these faunas are:

1. Dominance or sub-dominance of arctic species – *Curtonotus alpinus*, *Pterostichus costatus*, *P. sublaevis* and the rove beetle *Tachinus* cf. *arcticus* (Table 2).
2. Dominance or sub-dominance of sub-arctic species of the sub-genus *Cryobius* and the species *Pterostichus pinguedineus, P. ventricosus, Diacheila polita, Curtonotus torridus* (Table 2).
3. Single occurrences of sub-boreal steppe species – *Carabus sibiricus*, leaf beetles *Chrysolina perforata, Ch. aeruginosa*. Only one elytrum of a specimen of *Poecilus ravus* was found in the Aganskyi uval-1290/2 site (61°22'N, 76°45'E).

Entomo-complexes referred to as "arctic" allow the reconstruction of severe environmental conditions similar to the modern arctic tundra, characterized by a cold climate with temperatures of July +12°C, January -27°C, the distribution of open landscapes and the absence of wood.

Between 61° and 59°N, the fossil beetle faunas of the sub-arctic type are similar to the recent communities of the south tundra and forest tundra (sites 4–7 in Table 1). The main characteristics of these faunas are:

1. Presence of arctic species – *Curtonotus alpinus, Pterostichus costatus* and the rove beetle *Tachinus* cf. *arcticus* (but in fewer quantities than in arctic faunas).
2. Dominance of sub-arctic species presented by the sub-genus *Cryobius* of genus *Pterostichus, Pterostichus pinguedineus, Curtonotus torridus, Diacheila polita* (Table 2).
3. Occurrence of sub-boreal steppe species – *Carabus sibiricus, Poecilus ravus,* the weevil *Stephanocleonus eruditus*, and the carrion beetle *Aclypaea sericea.*

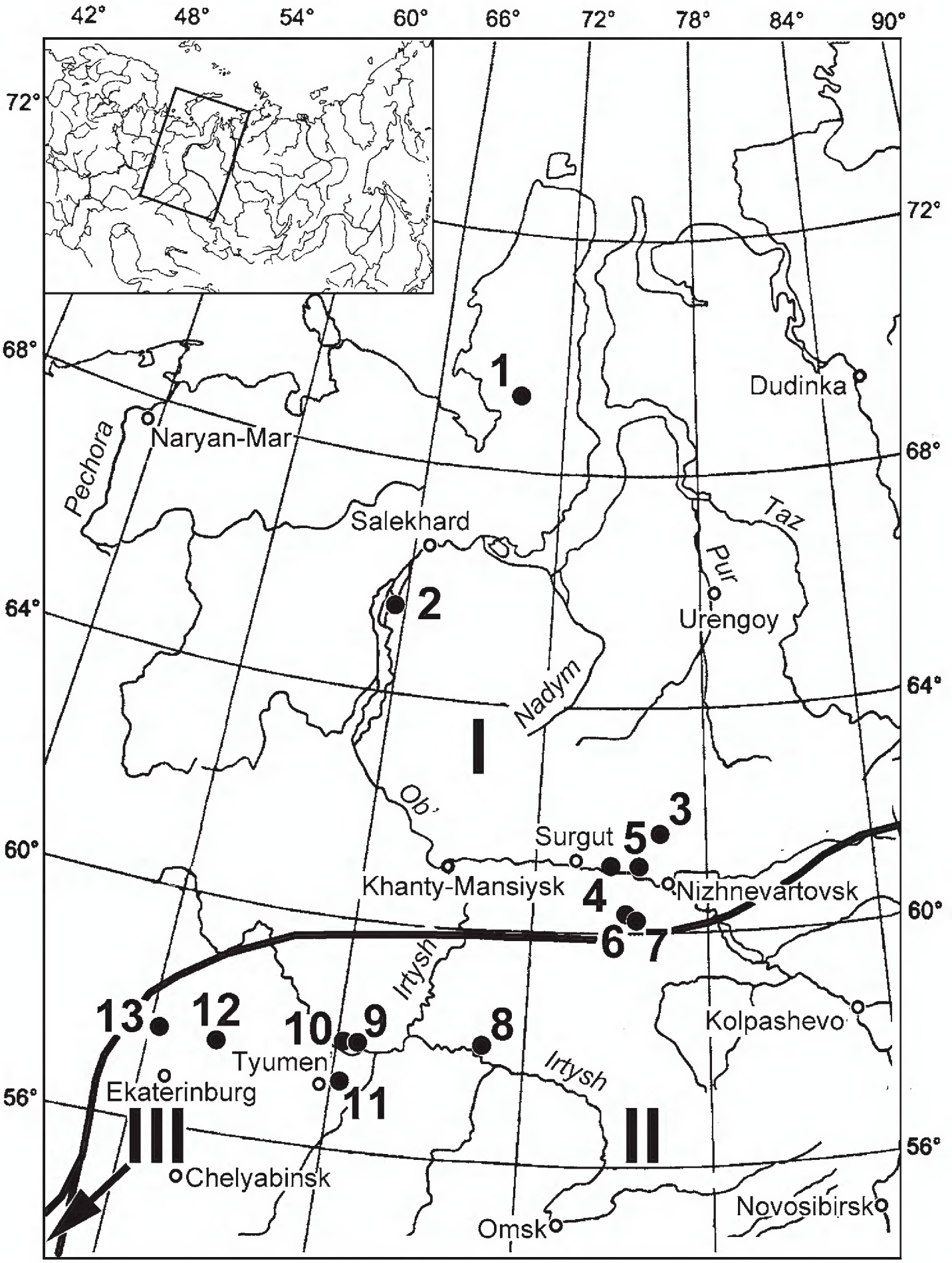

Figure 1. Geographical location of the study sites in the Ural Mountains and Western Siberia. Numbers of sites: **1** Syoyakha-Mutnaya **2** 430 km from Ob **3** Aganskiy uval-1290/2 **4** Mega **5** Lokosovo **6** Kul'egan-2247 Point I **7** Kul'egan -2247 Point II **8** Skorodum **9** Andriyshino **10** Nizhnyaya Tavda **11** Mal'kovo **12** Nikitino **13** Shurala.

▬▬ - Borders of vegetation types, reconstructed for the beginning of MIS 2 on the basis of palynological data: **I** periglacial tundra **II** periglacial steppe and forest-steppe **III** boreal forest and parklands (after Grichuk and Borisova 2009)

4. Presence of single xylophagous beetles associated with larch or spruce, the weevil *Callirus albosparsus*, and the bark beetle *Phoelotribus spinulosus*.

Insect assemblages referred to as belonging to the "sub-arctic" type, are similar to modern insect faunas from the southern part of the contemporary Sub-arctic. Presumably, reconstructed landscapes look like modern south tundra or forest tundra with the presence of single trees, such as larch or spruce. The thermal regime is probably characterized by several temperatures: July +13° – +14°C, January -25° – -26°C. These reconstructions are confirmed by palaeo-botanical data.

The faunas from sites situated south of 59°N are of a "mixed" type characterized by species combinations not presently found together; insect complexes of the majority of these localities resemble each other, with main features:

1. Dominance or sub-dominance of weevils *Otiorhynchus* similar to *O. politus*.
2. Presence of arctic and sub-arctic species – *Pterostichus* (*Cryobius*) spp., *Curtonotus alpinus*, the carrion beetle *Aclypaea sericea.*
3. Presence of sub-boreal steppe and sub-alpine insects – *Poecilus* (*Derus*) spp., *Cymindis mannerheimi, Pseudotaphoxenus dauricus*.
4. Occurrence of some halophylous beetles – *Pogonus* spp., darkling beetles *Belopus* spp.
5. Occurrence of xylophagous beetles (e.g., the bark beetle *Phoelotribus spinulosus*).

These faunas have no analogues among modern insect complexes, and may be classified as indicative of tundra steppe, although their species composition differs from that known from relict tundra steppe communities found today in Eastern Siberia and described by Berman (2001).

Discussion

Interpretation of the beetle communities

At first, these faunas suggest cooler than present climatic conditions, which is confirmed by the occurrence of sub-arctic species (*Pterostichus* (*Cryobius*) cf. *pinguedineus*, *P. ventricosus*, *Curtonotus torridus* and the arctic species (*Curtonotus alpinus*). This shows their southward distribution relative to their modern ranges.

As evidence of the lack of dense forest, is an absence of such typically boreal beetles as *Calathus micropterus*, *Pterostichus adstricus*, *P. oblongopunctatus* and others inhabiting the forest litter; at present they are widely distributed in the vast territories of West Siberia. Single boreal species are rare in the "mixed" faunas and are represented mainly by bark beetles (for example, *Phoelitribus spinulosus*, associated with spruce). The presence of sub-boreal beetles, inhabiting modern East-Siberian steppes (*Poecilus ravus*, *P. hanhaicus*) and sub-alpine grasslands (*Cymindis mannerheimi*) could indicate open landscapes. An abundance of weevils of the genus *Otiorhynchus* may be explained by the

Table 1. Chronological position of the study sites dated by the end of the Middle Pleninglacial period and associated with the "mammoth fauna".

Sites where sub-fossil insect faunas were found			Coordinates		Radiocarbon data, years before present (yr. BP). The abbreviation of organization and laboratory number of this data are given in parenthesis	
			N	E		
1.	Syoyakha-Mutnaya (V.I.Nazarov, unpublished data)		72°25'	66°48'	30,700±1100	(UPI-716)
2.	430 km of Ob		64°25'	70°50'	24,000±1500	(IPAE-63)
3.	Aganskiy uval-1290/2		61°22'	76°45'	23,300±575	(IPAE-95)
4.	Mega-2172		60°56'	72°20'	33,100±2300	(IOAN 132)
			60°56'	72°20'	26,285±590	(SOAN 982)
5.	Lokosovo		60°40'	71°32'	22,930±650	(SOAN 956)
6.	Kul'egan-2247 Point I		60°25'	75°50'	21,815±225	(SOAN-6837)
7.	Kul'egan -2247 Point II		60°25'	75°50'	26,730±250	(LOIA-8663)
8.	Skorodum		57°47'	70°58'	26,500±550	(SOAN 4538)
9.	Andriyshino		57°41'	66°08'	approximately 30,000 C14 yr. BP	
10.	Nizhnyaya Tavda		57°41'	66°12'	27,400±335	(SOAN 4534)
			57°41'	66°12'	24,820±750	(SOAN 4535)
11.	Mal'kovo		56°25'	66°10'	31,800±350	(GIN-5338)
12.	Nikitino		57°34'	63°17'	24,480±550	(SOAN 4537)
			57°34'	63°17'	28,460±800	(SOAN 4536)
13.	Shurala	Plant detritus	57°28'	60°15'	27,600±150	(Ki-15505)
		Mammalian bone	57°28'	60°15'	36,700±250	(Ki-15512)

wide distribution of herbal meadow vegetation. These faunas differ from contemporary insect steppe communities by the lack of darkling beetles, occurring in modern steppes and forest steppes (*Oodescelis polita*, *Crypticus quisquilius*, *Platyscelis hypolita*, *Opatrum riparium* etc.); it is possible that their absence was a result of cold climatic conditions.

At the same time, the presence of halophylous species, such as ground beetles of the genus *Pogonus*, darkling beetles of the genus *Belopus*, may indicate local soil salinity. At present these halophilic species are distributed southwards from 56–57°N and are very rare between 57–58°N, situated in sites with "mixed" faunas. Moreover, I am not aware of the presence of halophilic species of the genera Pogonus and Belopus in Central and East Siberia.

It may be assumed that such faunas inhabited open communities which can be defined as "cool grasslands" with a presence of rarefied forests or of single trees and local soil salinity. Similar conclusions have been drawn from palaeo-botanical data obtained at the same sites: they show a dominance of herbal vegetation with an abundance of cereals, wormwoods and chenopodiaceous plants.

The occurrence of some boreal faunas in single sites (Niznyaya Tavda, C^{14} 27,400 ± 335 yr. BP) do not contradict the overall distribution of open landscapes, and show the presence of isolated patches of forest vegetation, like in modern forest steppes.

Therefore, entomological data show that at the time of the terminal phase of Middle Pleninglacial the following types of landscapes were distributed in the territories of the Ural Mountains and West Siberia: the northern part of the region north of 61°N was dominated by open landscapes similar to modern tundra, between 64 and 62°N - similar to forest tundra and between 59 and 57°N – non-analogue landscapes, which may be defined as "open grasslands" or savannas with a presence of rarefied forests.

The main influence on the natural ecosystems came from palaeo-environmental factors. The Middle Weichselian Interstadial was characterized by a continental and a cooler-than-present climate with low winter temperatures and a wide distribution of permafrost; the resulting development of large ice sheets caused a strong drying effect. Decreasing sea levels provided the opening of sea shelves and the connection between Europe and the British Isles, and the Beringian Bridge between Siberia and Alaska. Cold and dry climatic conditions reconstructed for main territories of Europe, even for the Mediterranean region (Adams and Faure, 1997) may have caused a wide distribution of open landscapes such as tundra steppes of grasslands corresponding with the periglacial zone or "hyperzone" (Velichko 1973). Palaeoenvironmental reconstructions of "mixed" insect faunas from localities situated in the Ural Mountains and West Siberia show the presence of landscapes similar to savannas with rarefied woody vegetation. According to palaeo-botanical data (Stefanovsky et al. 2007), these "mixed" faunas correspond with open plant associations with an abundance of herbal vegetation.

It is necessary to define which factors might prevent the distribution of woods in the period of the Late Pleistocene studied. The main environmental factor is climate as a combination of thermal regime, precipitation, insulation, etc. At present I can suggest that severe climatic conditions similar to the palaeo-environment of the terminal phase end of the Middle Pleninglacial in the Central part of North Eurasia between 59° and

Table 2. Species of beetles found in the study sites associated with the "mammoth fauna".

Type of range*	Taxon	Sites (see Table 1)												
		1	2	3	4	5	6	7	8	9	10	11	12	13
	COLEOPTERA:													
	Carabidae:													
a-sb	*Carabus sibiricus* F.-W.						+	+					+	
a-sb	*C.* cf. *sibiricus* F.-W.		+											
	C. (*Trachycarabus*) sp.									+				
a	*C. truncaticollis* Esch.			+										
a	*C.* cf. *truncaticollis* Esch.		+											
sa	*C.* cf. *odoratus* F.-W.		+											
	C. (*Morphocarabus*) sp.							+						
	C. sp.		+	+					+	+			+	+
p	*Nebria rufescens* Sturm						+							
sa	*N. nivalis* Payk.							+	+					
	N. sp.	+												
sa	*Pelophila borealis* Payk.		+				+	+	+	+	+	+	+	
p	*Elaphrus riparius* L.		+											
p	*Notiophilus* cf. *aestuans* Motsch.													+
p	*N.* cf. *aquaticus* L.			+		+	+	+	+	+			+	
b	*N. reitteri* Spaeth								+		+			
b	*N. biguttatus* F.								+					
	N. sp.							+	+	+	+		+	
sa	*Blethisa catenaria* Brown.		+		+		+	+						
p	*B. multipunctata* L.				+									
sa	*Diacheila polita* Fald.	+	+	+	+		+	+	+	+	+	+	+	
sa	*D. arctica* Gyll.				+					+				
p	*Elaphrus riparius* L.				+			+	+				+	
sa	*E. lapponicus* Gyll.								+					
b	*E. angusticollis* R. F. Sahlb.						+	+	+					
b	*E.* cf. *angusticollis* R. F. Sahlb.								+					
	E. sp.						+			+				
p	*Lorocera pilicornis* F.													+
p	*Clivina fossor* L.							+		+				+
p	*Dyschiriodes* cf. *globosus* Hbst.													+
	D. sp.								+	+			+	
b	*Trechus secalis* Payk.										+			
b	*T. rivularis* Gyll.						+	+						
b	*Bembidion striatum* F.								+				+	
b	*B. velox* L.								+					
sa	*B. captivorum* Net.						+							
sa	*B. scandicum* Lindr.						+							
b	*B. ovale* Motsch.						+							
sa	*B. umiatense* Lindr.								+					
sa	*B.* cf. *umiatense* Lindr.							+	+	+				

Type of range*	Taxon	Sites (see Table 1)												
		1	2	3	4	5	6	7	8	9	10	11	12	13
b	*B. infuscatum* Dej.									+	+			
b	*B.* cf. *infuscatum* Dej.									+				
sa	*B. grapei* Gyll.								+				+	
sa	*B.* cf. *grapei* Gyll.							+		+				
b	*B. scopulinum* Kby.												+	
b	*B. deletum* Serv.								+					
b	*B.* cf. *deletum* Serv.								+					
p	*B.* cf. *tetracolum* Say									+				
	B. (*Ocydromus*) sp.						+	+	+	+			+	+
sa	*B. fellmanni* Mnnh.												+	
sa	*B.* cf. *fellmanni* Mnnh.						+	+		+				
	B. (*Plataphodes*) sp.							+	+				+	
p	*B. obliquum* Ol.													+
	B. (*Bembidionetolitzkya*) sp.												+	
	B. sp.			+				+	+	+	+		+	+
sb	*Pogonus* cf. *punctatulus* Dej.												+	
sb	*P.* cf. *cumanus* Lutschn.								+					
sb	*P.* cf. *meridionalis* Dej.								+	+				
sb	*P.* cf. *transfuga* Chaud.									+				
sb	*P.* sp.								+	+		+	+	+
p	*Patrobus septentrionis* Dej.			+			+	+	+	+			+	
p	*P. assimilis* Chd.								+				+	
sb	*Poecilus major* Motsch.										+			+
sb	*P.* cf. *major* Motsch.									+		+		
sb	*P. ravus* Lutshn.			+			+	+	+	+	+	+	+	
sb	*P.* cf. *ravus* Lutshn.								+	+			+	
sb	*P. hanhaicus* Tsch.									+				
sb	*P.* cf. *hanhaicus* Tsch.								+	+			+	
sb	*P.* (*Derus*) sp.								+	+				
t	*P. lepidus* Leske								+					
	P. (*s.str*) sp.							+					+	
p	*Pterostichus nigrita* F.			+			+							
b	*P. mannerheimi* Dej.			+										
b	*P. maurusiacus* Mnnh							+						
b	*P.* cf. *maurusiacus* Mnnh							+						
sa	*P. parens* Tsch.							+						
	P. (*Eosteropus*) sp.			+					+					
sa	*P. montanus* Motsch.						+	+						
sa	*P.* cf. *montanus* Motsch.		+											
sa	*P. kokeili* ssp. *archangelicus* Popp.						+							
sa	*P. tundrae* Tsch.		+	+			+	+						
sa	*P.* cf. *tundrae* Tsch.			+				+						
sa	*P.* cf. *abnormis* J.R.Sahlb.							+						
	P. (*Petrophilus*) sp.			+				+	+	+				

Type of range*	Taxon	Sites (see Table 1)												
		1	2	3	4	5	6	7	8	9	10	11	12	13
sa	*P. agonus* Horn.		+				+							
a	*P. vermiculosus* Men.	+	+	+	+		+	+						
a	*P.* cf. *cancellatus* Motsch.		+											
a	*P. costatus* Men.		+	+	+		+	+						
a	*P. sublaevis* J.R.Sahlb.		+	+			+	+						
sa	*P. tareumiut* Ball.					+								
sa	*P.* cf. *tareumiut* Ball.						+							
sa	*P. theeli* Maekl.					+								
sa	*P.* cf. *theeli* Maekl.						+							
sa	*P. middendorfii* J.Sahlb.						+	+						
sa	*P.* cf. *middendorffi* J.R.Sahlb.							+	+	+				
sa	*P. ventricosus* Esch.			+			+	+					+	
sa	*P.* cf. *ventricosus* Esch.		+	+									+	
sa	*P. pinguedineus* Esch.	+				+								
sa	*P.* cf. *pinguedineus* Esch.		+	+				+	+	+			+	
sa	*P.* cf. *nigripalpis* Popp.	+		+										
sa	*P. negligens* Sturm.			+			+	+		+		+	+	
sa	*P.* cf. *negligens* Sturm		+							+				
sa	*P. brevicornis* Kby.			+		+	+	+		+			+	
sa	*P.* cf. *brevicornis* Kby		+						+					
sa	*P.* (*Cryobius*) sp.	+	+	+	+		+	+	+	+	+		+	+
b	*P. diligens* Sturm						+	+	+				+	
b	*P.* cf. *diligens* Sturm								+	+				
b	*P.* cf. *strenuus* Panz.									+				+
b	*P.* (*Phonias*) sp.				+			+		+				
	P. sp.		+	+					+	+			+	+
sa	*Stereocerus haematopus* Dej.		+	+			+	+		+				
sa	*S.* cf. *haematopus* Dej.							+						
sa	*S. rubripes* Motsch.							+						
sa	*S.* cf. *rubripes* Motsch.						+	+						
sa	*S.* sp.						+							
	Platynus sp.								+	+				
sa	*Agonum alpinum* Motsch.												+	
p	*A.* cf. *versutum* Sturm												+	
p	*A. ericeti* Panz.				+		+							
p	*A. micans* Nic.								+					
p	*A.* cf. *gracile* Gyll.						+							
	A. (*Europhilus*) sp.								+					
	A. sp.	+		+			+	+		+	+			
b	*Synuchus vivalis* Payk.			+										
sb	*Pseudotaphoxenus dauricus* F.-W.									+				
sa	*Amara quenseli* Shoenh.						+						+	
a	*A. glacialis* Mnnh.						+	+						
sa	*A. erratica* Duft.							+		+				

Type of range*	Taxon	Sites (see Table 1)												
		1	2	3	4	5	6	7	8	9	10	11	12	13
b	*A. minuta* Motsch.							+						
sa	*A. interstitialis* Dej.						+	+	+		+			
b	*A. brunnea* Gyll .			+				+		+			+	+
b	*A.* cf. *brunnea* Gyll.							+						
	A. (*Bradytus*) sp.								+					
	A. (*Celia*) sp.								+					
	A. sp.						+	+	+	+			+	
sa	*Curtonotus hyperboreus* Dej.								+					
a	*C. alpinus* Payk.		+	+		+	+	+		+				
a	*C.* cf. *alpinus* Payk.									+				
sa	*C. torridus* Panz.					+		+	+	+			+	
sa	*C.* cf. *torridus* Panz.		+					+	+	+				
sb	*C. dauricus* Motsch.									+				
	C. sp.		+	+				+	+	+	+			
sa	*Harpalus nigritarsis* C.R.Sahlb.							+	+	+			+	
sa	*H.* cf. *nigritarsis* C.R.Sahlb.								+				+	
sb	*H.* cf. *pulvinatus* Men												+	
	H. sp.								+	+				
sa	*Dicheirotrichus mannerheimi* R. F. Sahlb.						+	+	+	+				
sb	*Cymindis mannerheimi* Gebl.									+		+	+	
sa	*C. macularis* F.-W.								+	+				
b	*C.* cf. *rivularis* Motsch.									+				
	Cymindis sp.								+	+				
	Carabidae indet.			+			+	+						
	Dytiscidae:													
	Agabus (*Gaurodytes*) sp		+	+	+		+	+					+	
	Agabus sp.							+	+	+			+	+
	Hydroporus sp.	+					+		+		+			
	Dytiscidae indet.						+	+						
	Gyrinidae:													
	Gyrinus sp.			+					+					
	Hydrophilidae:													
p	*Hydrobius fuscipes* L.			+				+	+					
p	*Helophorus* cf. *nubilis* F.	+												
sa	*H. obscurellus* Popp.						+							
sa	*H.* cf. *obscurellus* Popp.								+					
	H. sp.		+				+	+	+	+	+		+	
	?*Helophorus* sp.							+						
	Cercyon sp.				+		+	+	+	+	+		+	
	Histeridae:													
	Margarinotus sp.								+					
	Catopidae:													
	Catops sp.		+	+		+	+	+	+		+			

Type of range*	Taxon	Sites (see Table 1)												
		1	2	3	4	5	6	7	8	9	10	11	12	13
	Colon sp.									+				
	Silphidae:													
sb	*Aclypaea sericea* Zoubk.								+					
sb	*A. bicarinata* Gebl.								+		+			
p	*A. opaca* L.						+	+	+	+	+		+	
	Thanatophilus sp.			+			+		+					
	Liodidae:													
	Agathidium sp.			+			+		+	+	+		+	
	Anisotoma sp.			+										
	Liodes sp.							+	+	+	+			+
	Staphylinidae:													
p	*Acidota crenata* Mnnh.										+			
p	*A.* cf. *cruentata* Mnnh.						+							
	A. sp.										+			
	Olophrum sp.			+			+		+					+
	Omaliinae gen. sp.	+	+	+				+	+	+	+		+	
a	*Tachinus* cf. *arcticus* Maekl.	+	+	+		+	+	+	+					
	Omaliinae gen. sp.													
	Ocypus sp.									+				
	Oxythelinae gen. sp.									+	+			
	Tachinus sp.			+	+			+	+	+			+	
	?*Mycetoporus* sp.								+					
	? *Philonthus* sp.		+											
	Tachyporinae gen. sp.			+							+			
	Stenus sp.			+			+	+	+					
	Lathrobium sp.			+			+				+			+
	Paederinae gen sp.			+					+		+			
	Quedinus sp.			+					+					+
p	*Scaphisoma* sp.						+							
	Staphylinidae indet.			+	+	+	+	+						
	Scarabaeidae:													
t	*Aphodius distinctus* Müll.								+					
t	*A.* cf. *distinctus* Müll.						+	+	+				+	
t	*A.* cf. *melanostictus* W.Schm.							+		+	+			
t	*A.* cf. *fossor* L.								+		+			
t	*A.* cf. *brevis* Er.								+		+			
t	*A.* cf. *rufipes* L.												+	
	A. sp.			+			+	+	+	+	+		+	
p	*Aegialia abdita* Nikritin							+	+	+	+		+	
	Helodidae:													
	Cyphon sp.							+			+			
	?*Cyphon* sp.													
	Dermestidae:													
	Dermestidae indet.								+					
	Byrrhidae:													

Type of range*	Taxon	Sites (see Table 1)												
		1	2	3	4	5	6	7	8	9	10	11	12	13
	Byrrhus sp.	+							+		+		+	
sb	*Porcinolus murinus* F.								+	+				
sa	*Morychus viridis* Kuzm. et Kor.			+			+	+			+			
sa	*M.* cf. *viridis* Kuzm. et. Kor.								+					
	M. sp.		+							+			+	
	Simplocaria sp.			+	+		+	+	+				+	
	Curimopsis sp.			+										
	Byrrhidae gen. sp.			+					+					
	Anobiidae:													
p	*Caenocara bovistae* Hoffm.			+			+							
	Heteroceridae:													
	Heteroceris sp.			+										
	Elateridae:													
p	*Hypnoidus* cf. *rivularis* Gyll.							+						
	H. sp.			+						+				
	Nitidulidae:													
	Nitidulidae gen. indet.								+	+	+			
	Cryptophagidae:													
	Cryptophagidae indet.						+							
	Erotylidae:													
	Erotylidae indet.												+	
	Coccinellidae:													
b	*Scymnus* sp.									+				
sa	*Hippodamia arctica* Schneider									+				
b	*Coccinella* trifasciata L.							+						
b	*C.* cf. *hieroglyphica* L.									+				
b	*C.* sp.									+				
	Latridiidae:													
	Latridiidae gen.sp.	+									+			
	Oedemeridae:													
	Oedemeridae gen. sp.			+										
	Anthicidae:													
	Anthicidae gen.sp.										+			
	Tenebrionidae:													
sb	*Belopus* sp.								+					
	Chrysomelidae:													
	Donacia sp.	+					+							
sb	*Chrysolina perforata* Gebl.									+				
sb	*Ch.* cf. *perforata* Gebl.		+											
sb	*Ch.* cf. *aeruginosa* Fald.		+											
a	*Ch.* cf. *cavigera* J.R.Sahlb.		+											
a	*Ch.* cf. *subsulcata* Esch.		+	+										
sa	*Ch. septentrionalis* Men.		+											
sa	*Ch.* cf. *septentrionalis* Men							+						

Type of range*	Taxon	Sites (see Table 1)												
		1	2	3	4	5	6	7	8	9	10	11	12	13
p	*Ch.* cf. *graminis* L.								+					
	Ch. sp.		+	+			+	+	+	+				
a	*Chrysomela* cf. *taimyrensis* L. Medv.		+											
	Ch. sp.			+		+	+	+		+	+		+	
sb	*Colaphellus sophiae* Schall.								+	+	+			
p	*Hydrothassa hannoverana* F.												+	
	Phaedon sp.		+							+				
p	*Plagoiodera versicolora* Laich.		+						+					
	Crosita sp.							+	+					
	Phratora sp.			+										
	Chalcoides sp.								+					
	?*Chalcoides* sp.								+					
	?*Chaetocnema* sp.								+					
	Altica sp.			+										
	Alticinae gen. sp.			+										
	Chrysomelidae indet.			+		+								
	Erirhinidae:													
p	*Tournotaris bimaculatus* F.			+			+	+	+	+	+	+	+	+
b	*T. ochoticus* Kor.						+	+						
b	*T.* cf. *ochoticus* Kor.													+
p	*Notaris aethiops* F.						+	+		+	+			+
	N. sp.	+					+		+				+	
	Curculionidae:													
sb	*Otiorhynchus unctuosus* Germ.										+			
b	*O. politus* Gyll.									+	+	+		+
b	*O.* cf. *politus* Gyll.								+	+	+	+	+	+
sb	*O. wittmeri* Legalov									+				
sb	*O.* cf. *wittmeri* Legalov									+				
sa	*O.* cf. *arcticus* F.		+											
p	*O. ovatus* L.										+			
p	*O.* cf. *ovatus* L.										+			
	O. sp.						+		+	+	+		+	+
sa	*Sitona* cf. *ovipennis* ssp.*borealis* Kor.		+				+							
	S. sp.	+									+			
b	*Chlorophanus* cf. *sibiricus* Gyll.										+			
	Ch. sp.						+							
?p	*Phyllobius* cf.*crassipes* Motsch et *maculicornis* Germ.			+										
	Ph. sp.						+	+	+	+	+		+	
	Strophosoma sp.							+						
sb	*Eusomus ovulum* Germ.													+
a-sb	*Coniocleonus ferrugineus* Fahr										+		+	+

Type of range*	Taxon	Sites (see Table 1)												
		1	2	3	4	5	6	7	8	9	10	11	12	13
a-sb	*C.* cf. *ferrugineus* Fahr		+											
	C. sp.		+							+				+
a-sb	*Stephanocleonus eruditus* Fast.						+							
	S. sp.										+		+	
sb	*Bothynoderes foveocollis* Gebl.										+			
	Cleoninae indet.					+	+	+	+	+			+	
p	*Hypera rumicus* L.							+						
p	*H.* cf. *ornata* Cap.		+				+	+						
p	*H. elongata* Pk.			+										
	H. sp.			+	+	+	+	+	+	+	+		+	+
sa	*Lepyrus nordenskjoldi* Faust.						+	+						
sa	*L.* cf. *nordenskjoldi* Faust		+	+										
sa	*L.* cf. *arcticus* Pk.	+												
	L. sp.					+	+	+					+	
b	*Trichalophus maeklini* Faust		+											
	T. sp.													+
p	*Phytobius* cf. *velaris* Gyll.		+		+									
b	*Callirus albosparsus* Boh.						+							
b	*C.* sp.										+			
b	*Pissodes* sp.							+			+			
	Bagous sp.						+			+				
	?*Limnobaris* sp.								+					
b	?*Magdalis* sp.												+	
b	*Rhyncholus ater* L.										+			
	Anthonomus sp.									+	+			
p	*Dorytomus* cf. *imbecillus* Faust							+						
	D. sp.							+		+	+			+
p	*Ceutorrhynchus* cf. *erysimi* F.						+							
	C. sp.						+	+					+	
p	*Isochnus saliceti* Müll	+												
sa	*I. arcticus* Kor.			+				+						
	Rhynchaenus sp.		+		+				+	+	+			
	Curculionidae indet.						+	+						
	Brentidae:													
sa	*Hemitrichapion tschernovi* T.-M.			+	+		+	+						
	H. sp.													
p	*Mesotrichapion* cf. *punctirostre* Gyll.						+	+						
p	*Betulapion simile* Kby									+			+	
p	*B.* cf. *simile* Kby.			+										
	Cyanapion sp.									+				
	Brentidae gen.sp.	+	+	+			+	+		+	+		+	
	Scolytidae:													
b	*Phoelotribus spinulosus* Rey.							+	+		+		+	
b	*Polygraphus* sp.								+					

57°N are presented in the inner parts of Central and East Siberia. However, the modern conditions of cool and continental climate cannot avert the present distribution of woodland vegetation in this area. I suggest that not only climatic factor prevented of the distribution of woods in the central part of northern Eurasia between 59° and 57°N. Apart from climate, other factors might influence Pleistocene ecosystems; these factors may have impeded reforestation and stimulate the distribution of open landscapes.

The influence of mammoths and other large herbivorous mammals representing the "mammoth fauna" is probably large. It is known that vast areas of the continent were occupied by mammals belonging to the mammoth complex at that time (Markova et al. 2008).

Evidence for the co-occurrence of insects with mega mammals of the "mammoth" fauna

Firstly, in many sites fossil insects were found along with mammoth remains (*Mammuthus primigenius*) and other large herbivorous mammals (teeth, tusks, fragments of cranium, etc.) (Borodin et al. 2001).

Secondly, in the majority of sites fragments of dung beetles of the genus *Aphodius*, were found which suggests the presence of mammoths and other large herbivorous mammals in the same landscapes (Sher and Kuzmina 2007).

According to the literature, mammoths and other mega mammals such as woolly rhinoceros (*Coelodonta antiquitatis*), giant deer (*Megaloceros giganteus*), reindeer (*Rangifer tarandus*), wild ox (*Ovibos moschatus*), primitive bison (*Bison priscus*) and some others may be considered as an additional factor, which influenced Late Pleistocene ecosystems (May 1993; Puchkov 2001).

Mammoths and other mammals were indicators of certain communities, and preserved specific ecosystems (Puchkov 2001):

1. Destruction of undergrowth and feeding impeded reforestation and might preserve herbal communities.
2. The hooves of mammoths destroyed the moss turf; as a result, moss cover disappeared in the territories of modern taiga and tundra zones, being replaced by mezo- and xerophylous herbal vegetation.

That is, mammoths and other mega mammals could rarefy forests and promote the distribution of zoogenic herbal vegetation consisting of cereals (Stuart and Hibbard 1986; Stuart 1991; May 1993; Puchkov 2001).

Consequently, Pleistocene forests were rare, and meadow and steppe plants were significant in the Siberian ecosystems.

I therefore suggest that the species composition of insects was affected by two important factors:

1. Cool and dry climate which caused low winter temperatures and a wide distribution of permafrost.

2. Pasture of large herbivorous mammals (mammoth and accompanying species) which caused the formation of «pasture» savannas with an abundance of herbal vegetation and rare forests.

Do these factors define the composition of insect complexes as "mixed" faunas at 59°–56°N?

Firstly, cool and dry climate may cause a southward advance of arctic and sub-arctic species (*Diacheila polita*, *Curtonotus alpinus*, *C. torridus*, *Pterostichus* (*Cryobius*) spp.). As such, the warming and drying of local habitats (such as slopes with a southern exposition) in dry and cold climatic conditions and their subsequent salinity may cause the occurrence of some halophilic beetles.

Secondly, the pasture of mammoths and other mega mammals may cause the distribution of grasslands with a dominance of cereals and an abundance of weevils of the genus *Otiorhynchus*. The presence of sub-boreal steppe and sub-alpine species (*Poecilus ravus*, *Cymindis mannerheimi*, *Chrysolina perforata*) may have been caused by both environmental conditions and pasturable load. Rarefaction of woods may explain the lack of species inhabiting forest litter (*Calathus micropterus*, *Pterostichus oblongopunctatus* etc.); presence of single trees - occurrences of xylophagous beetles (bark beetle *Phoelotribus spinulosus* etc.). The fertilization of the soil may have caused the occurrence of coprophagous beetles (dung beetles of the genera *Aphodius*).

A combination of these factors may have caused the distribution of several landscapes.

In the central and northern parts of the region north of 59°N, the cold climate and corresponding mammoth pasture formed communities similar to modern tundra and forest tundra. South of 59°N and up to 57°N, specific landscapes and according insect faunas were formed. These conclusions do not contradict literature data on the palaeo-geography of that period (Arkhipov and Volkova 1994; Volkova et al. 2005; Astakhov 2009).

It may be assumed, that ground beetles of the species *Carabus sibiricus, Poecilus ravus, Pterostichus pinguedineus, Cymindis mannerheimi* and others have been widely distributed in the territories of the central part of Northern Eurasia, so that these insects may form an integral part of the landscapes containing the "mammoth faunas".

Factors leading to the disappearance of the "mammoth faunas"

At the beginning of the Holocene (10,000 yr. BP) in the Northern Hemisphere significant climatic changes took place, modifying all natural communities, and the final degradation of "mammoth faunas" took place. The largest mammals, mammoth (*Mammuthus primigenius*), woolly rhinoceros (*Coelodonta antiquitatis*), and giant deer (*Megaloceros giganteus*), having the greatest effect on terrestrial ecosystems, died out about 10–8,000 years ago, and the ranges of other species, such as reindeer (*Rangifer tarandus*), musk ox (*Ovibos moschatus*)) shifted either northwards to the

tundra and forest tundra, or southwards, to the steppes, such as the saiga antelope (*Saiga tatarica*).

The subsequent Early Holocene warming and humidification of climate, the extinction of mammoths and its consequent failing of the "pasture load" caused the reforestation and water logging of vast territories, the formation of the boreal belt, the transformation of the flora and fauna, and the wide distribution of conifer forests.

Therefore, climatic changes and the extinction of the large mammals happening between the Pleistocene and Holocene caused the disappearance of the "mixed" or non-analogue insect faunas. However, the insect species did not die out, but only changed the location of their ranges. At that time the "mixed" insect faunas disintegrated into groups of single species, shifting their ranges northwards (*Curtonotus alpinus, Pterostichus* (*Cryobius*) spp.), southwards (*Pogonus* spp., *Cymindis mannerheimi*) or eastwards (*Poecilus* (*Derus*) *hanhaicus*, *P.* (*Derus*) *ravus, P.* (*Derus*) *major, Pseudotahoxenus dauricus, Amara minuta*). These species only left the territories studied but could survive these environmental changes in other regions of northern Eurasia, such as Mongolia, Eastern Siberia, or the Pamir Mountains, where environmental conditions are more compatible to their ecological requirements.

Comparison with other regions of North Eurasia

The "mixed" or non-analogue faunas of the central part of North Eurasia were compared with synchronous insect faunas as described for East Siberia (Sher et al. 2005, Kuzmina and Sher, 2006; Sher and Kuzmina, 2007). Significant differences between these regional faunas were found. Firstly, in the Late Quaternary insect complexes of Northeastern Siberia with remains of the pill beetle *Morychus viridis* were found in large quantities. Moreover Sher and Kuzmina claimed that *Morychus viridis* is "… a real symbol of the Pleistocene biota in Northeastern Siberia" (Sher and Kuzmina, 2007, p. 105). Remains of *Morychus* similar to *M. viridis* were found in "mixed" faunas from the Ural Mountains and West Siberia, although these insects were not so numerous here. The MIS 3 insect assemblages of the study area characterized by an abundance of fragments of weevils of the genus *Otiorhynchus* and morphologically similar to *O. politus* did not occur in the East Siberian sub-fossil insect faunas. The steppe assemblages of fossil insects from East Siberia belong to species, which are not found in the "mixed" insect faunas of the Ural Mountains and West Siberia, such as weevils of the genus *Stepanocleonus* (*S. eruditus, S. fossulatus*), *Poecilus nearcticus, Harpalus vittatus*. Tundra steppe beetles, such as *Troglocollops arcticus,* and *Galeruca interrupta circumdata* were not found in the insect assemblages of the Ural Mountains and West Siberia. An important feature of these "mixed" faunas of the Central part of North Eurasia is the presence of halophilic beetles which indicates local soil salinity, which may be explained by a strong aridity of the climate and by an external biogenic influence (pasture load) on the landscapes. No halophilic insects were found in fossil insect assemblages in Central and East Siberia. However, in East Siberian MIS 3 faunas

remains of dung beetles of the genus *Aphodius* were found, which are considered to indicate the presence of herbivorous mammals (Sher and Kuzmina, 2007).

Sub-fossil insect assemblages from Northeastern Siberia may reflect the existence of tundra steppe landscapes which have no analogue among modern ecosystems (Sher et al. 2005). The climate forming these communities can be considered as a main factor, but by cutting and trampling of grasses herbivores including large mammals made their own contribution to the formation of these ecosystems. For a long time pasture load allowed the perpetuation of grazing ecosystems (Zimov et al. 1995, Sher et al. 2005).

Insect faunas at the end of the Middle Pleninglacial in Western Europe (Bos et al. 2004) differ strongly from our faunas by the lack of steppe, by the absence of halophilic species and by the occurrence of the pill beetle of the genus *Morychus*. Weevils of the genus *Otiorhynchus* from European sites belong to *O. dubius,* which is not found in West Siberian faunas.

It is possible that these faunas, belonging to the "mixed" type, were distributed mainly in the Central part of North Eurasia (including West Siberia and the Ural Mountains) during the Late Pleistocene (MIS 4-MIS 2). So, similar faunas were found in the Gornova site, situated in the South Ural Mountains, near Ufa city (data given by F.G.Bidashko (Kazakhstan)). These assemblages are characterized by abundance of remains of the genus *Otiorhynchus* (similar to *O. politus*), the presence of *Poecilus ravus, Pogonus* spp., *Belopus* spp. and other species, with the presence of some endemic forms (*Nedria uralensis*).

Conclusions

1. Sub-fossil insect assemblages allow us to reconstruct several elements of the natural zonality which existed in the central part of Northern Eurasia during the terminal phase of the Middle Pleninglacial (MIS 3). In the northern and central parts of the region north of 59°N, the cold climate and the corresponding mammoth pasture formed communities similar to modern tundra and forest tundra. In the southern part of the study area between 57° and 59°N, specific landscapes and corresponding insect faunas formed, known as "mammoth savannas".
2. Insect faunas of a "mixed" type of the Ural Mountains and West Siberia differ from East Siberian sub-fossil insect assemblages found in synchronous layers with the presence of numerous fragments of weevils *Otiorhynchus* which are morphologically similar to *O. politus*, as well as the halophilic beetles of the genera *Pogonus* and *Belopus*. Steppe beetles, such as weevils of the genus *Stepanocleonus* did not establish assemblages in West Siberia. Significant differences between insect assemblages from the central part of northern Eurasia and Western Europe were marked too. These faunas cannot be identified both as forest tundra nor tundra steppe and differ even from modern insect communities of East Siberia relict tundra steppes.
3. The species composition of insect complexes was determined not only by climate, but by pasture pressure of mammoths and other herbivorous mammals as well. A pasture load occurred in all territories of the Ural Mountains and West Siberia,

but is defined differently in different parts of the study area. In the central and northern parts of the region north of 59°N, a combination of these factors formed communities similar to modern tundra and forest tundra in accordance to the southward advance of arctic and sub-arctic insect complexes relative to contemporary faunas. In those territories lying during the terminal phase of MIS 3 between 59° and 57°N insect faunas existed without any analogues among modern insect complexes and included sub-arctic, sub-boreal steppe species, halophilic insects and weevils of the genus *Otiorhynchus* and similar to *O. politus.*

Acknowledgements

The author thanks his colleagues at the Laboratory of Historical Ecology of IPAE – Dr. P. Kosintsev, Dr. A. Borodin, Dr. E. Kuzmina for discussions during the preparation of this article, Dr. A. Borodin, Dr. P. Kosintsev, Dr. V. Stefanovsky, Mr. S. Zykov - for their help with collecting fossil data, Mrs. O. Korona and Mrs. S. Trofimova for providing palaeo-botanical data, Dr. P. Kositsev and Mr. N. Erokhin – for their help in obtaining radiocarbon data. Special thanks to Dr Tijs van Kolfschoten (Leiden Univ., the Netherlands) and Hans Turin for improving and reviewing this manuscript. This work was supported by the Russian Foundation for Basic Research (project 10–04-96102-r_Ural_a).

References

Adams J, Maslin M, Thomas E (1999) Sudden climate transitions during the Quaternary. Progress in Physical Geography 23 (1): 1–36.

Adams J, Faure H (1997) Palaeovegetation maps of the world since the Last Glacial; an aid to archaeological understanding. Journal of Archaeological Science 24: 623–647. doi: 10.1006/jasc.1996.0146

Arkhipov SA, Volkova VS (1994) Geological History, Landscapes and Climates of the Pleistocene in West Siberia. Novosibirsk, Siberian Branch of the Russian Academy of Sciences, 105 pp. (In Russian).

Astakhov VI (2009) Main landmarks of the Late Pleistocene of the Ural-Siberian Arctic. Fundamental problems of Quaternary: results and trends of further researches: Proceedings of the VI All-Russian Quaternary Conference, October 19–23, 2009, Novosibirsk, 50–52. (In Russian)

Berman DI (2001) Tundra–steppes of Pleistocene Beringia and modern insects. Priroda 11: 22–33. (In Russian)

Borodin AV, Strukova TV, Trofimova SS, Zinoviev EV (2001) Reconstruction of mammoth environments at different stages of the Pleistocene in the West-Siberian Plain. In: Cavaretta G, Giola P, Mussi M, Palombo MR (Eds) The World of Elephants. Proceedings of the First International Congress. Consiglio Nazionale delle Ricerche, Rome, 267–271.

Bos JAA, Dickson J, Coope JR, Jardine, WG (2004) Flora, fauna and climate during the Weichselian Middle Pleninglacial – palynological, macrofossil and coleopteran investi-

gations. Palaeogeography, Palaeoclimatology, Palaeoecology 204: 65–100. doi: 10.1016/S0031-0182(03)00724-7

Grichuk VP, Borisova OK (2009) Vegetation. Late Pleistocene (maps 20–21). In: Velichko AA (Ed) Paleoclimates and paleoenvironments of extra-tropical regions of the Northern Hemisphere. Late Pleistocene – Holocene: Atlas-monograph. Moscow: GEOS Publ.: 70–78.

Kiselev SV (1987) Field sampling for entomological analysis. Complex Biostratigraphic Investidations: Manual. Moscow University Press: 21–26. (In Russian).

Kuzmina SA, Sher AV (2006) Some features of the Holocene insect faunas of northeastern Siberia. Quaternary Science Reviews 25: 1790–1820. doi: 10.1016/j.quascirev.2006.01.013

Markova AK, Puzachenko AYu, van Kolfschoten T (2008) Species composition and geographical position of the mammal assemblages in the North Eurasia during the end of middle Valdai (=middle Zyryanian - middle Vistulian) mega-interstadial. Faunae and florae of Northern Eurasia in the Late Cenozoic. Rifei Publ., Ekaterinburg-Chelyabinsk: 7–24. [In Russian, English abstract].

May T (1993) Beeinflussten Grossauger die Waldvegetation der pleistozanen Warmzeiten Mitteleuropas? Natur und Museum 123 (6): 157–170.

Puchkov PV (2001) Why mammoths did not extinct in the interglaciations? Mammoth: 200 year of study. Moscow: GEOS Publ.: 57–69. [In Russian]

Puchkov PV (1997) Were the mammoths killed by the warming? Kyiv: Schmalhausen Institute of Zoology, 81 pp. [In Russian]

Sher AV, Kuzmina SA (2007) Late Pleistocene Beetle Records from Northern Asia. In: Beetle Records/Late Pleistocene of Northern Asia. Elsevier: 94–115.

Sher AV, Kuzmina SA, Kuznetsova TV, Sulerzhitsky LD (2005) New insights into the Weichselian environment and climate of the Eastern-Siberian Artic, derived from fossil insects, plants, and mammals. Quaternary Science Reviews 24: 533–569. doi: 10.1016/j.quascirev.2004.09.007

Stefanovsky VV, Zinovyev EV, Trofimova SS, Korona OM (2007) The alluvial complexes in Lower Reaches of Tawda River (the Northern Transuralia). Ural's Geological Journal 56 (2): 5–25. [In Russian]

Stuart A (1991) Mammalian extinctions in the Late Pleistocene of Northern Eurasia and North America. Biological Review 66: 453–562. doi: 10.1111/j.1469-185X.1991.tb01149.x

Stuart A, Hibbard Ph (1986) Pleistocene occurrence of Hippopotamus in Britain. Quartarpalaeontologie 6: 209–218.

Velichko A (1973) Natural process in the Pleistocene. Moscow, Nauka Publishers. 256 pp. (In Russian).

Volkova VS, Khazina IV, Babushkin AE (2005) Stratigraphy of the Pleistocene in West Siberia and a paleoclimatic scale. In: Quarter-2005. Proceedings of 4th All-Russian Meeting on the Study of the Quaternary. Syktyvkar, 77–78. [In Russian)]

Zimov SA, Chuprynin VI, Oreshko AP, Chapin III FS, Reynolds JF, Chapin MC (1995) Steppe-tundra transition: an herbivore-driven biome shift at the end of the Pleistocene. The American Naturalist 146: 765–794. doi: 10.1086/285824

Zinovyev EV (2006) Problems of ecological interpretation of Quaternary insect faunas from the central part of northern Eurasia. Quaternary Science Reviews 25: 1821–1840. doi: 10.1016/j.quascirev.2006.01.017